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Historical evidence for context-dependent assessment of *Erigeron canadensis* invasions in an 18th-century European landscape

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Abstract

Understanding the historical roots of invasion science provides insights into early perceptions of invasive species, allows us to trace the evolution of the discipline over time, and helps contextualize modern research. This paper analyzes work by Christian Ludwig Krause, published 250 years ago, on the invasion of an 18th-century European landscape by *Erigeron* [*Conyza*] *canadensis* (Canadian horseweed), one of the most common invasive species today and a widespread agricultural weed. Here an analysis is conducted of the ecological consequences and underlying mechanisms Krause described, how he evaluated *E. canadensis* invasions in different land-use systems and how his insights align with existing knowledge. Krause identified copious seed production and long-distance dispersal by wind as key mechanisms for the formation of dominant stands on degraded sandy soils. He recognized various ecosystem services associated with population establishment, such as erosion control, increased soil fertility, and the facilitation of other species. While Krause highlighted the benefits of *E. canadensis* invasions for the recovery of degraded grasslands and fields, he also acknowledged this introduced species as a troublesome weed in gardens. Thus, Krause's work is not only an early report on the invasion of a cultural landscape subject to wind erosion but also an early example of a context-dependent invasion assessment, illustrating both positive and negative impacts of the same species in different environments. Krause's perspective may encourage current assessments of *E. canadensis* not solely based on its presence or frequency, but on documented ecological and socioeconomic effects and their associated benefits or harms. As Krause impressively demonstrated 250 years ago, these effects can differ starkly in different environments, necessitating multiple responses to the same species.

Keywords

Agricultural weed, ecological restoration, ecosystem services, exotic species, history of invasion science, impact assessment, land degradation, plant invasion

Introduction

The establishment of invasion science as a discipline represents a remarkable achievement of the 20th century, and as the spread of non-native species accelerates, with associated challenges to biodiversity conservation, health, and economic sectors (Pyšek et al. 2020a; Zenni et al. 2021), the importance of the discipline grows. While the international SCOPE program on the ecology of biological invasions, which began in 1982, is often considered the foundation of modern invasion science (Simberloff 2011), the discipline has many historical roots. Elton's book from 1958 is a milestone (Richardson and Pyšek 2008), but invasion science has much deeper roots in Europe and elsewhere (e.g. van Wilgen 2020). In "The Origin of Species", for example, Darwin (1859) describes several invasion mechanisms (Ludsin and Wolfe 2001). Many other historical sources remain hidden, especially if they were not written in English. Acknowledging these roots allows us to better trace the evolution of the discipline over time and helps contextualize modern research.

Indeed, there are early works that describe some stages of the invasion process (as defined by Richardson et al. 2000), particularly species introduction, spread and naturalization. Since the Middle Ages, herbal books, garden directories, horticultural and forestry works have documented the influx of introduced species (e.g., Wein 1914). Starting at the end of the 17th century, regional floras and related works list species' spontaneous occurrences, providing documentation of their spread (e.g., de Tournefort 1698). In the 19th century, Watson (1847) and de Candolle (1855) developed initial frameworks, distinguishing native vs introduced plants and also addressing species' naturalization. Based on this, the Swiss botanist Thellung (1905, 1918/19) developed a comprehensive classification system that described species' introduction pathways and invasion success and applied it to regional floras. His "Flore adventive de Montpellier" (Thellung 1912) is a largely neglected milestone of bioecologically based invasion research, providing first quantifications for species' naturalization and the strength of introduction pathways (Kowarik and Pyšek 2012).

In ecological classifications (Richardson et al. 2000), species that have reached the fourth stage of the invasion processes by spreading beyond their point of introduction are considered "invasive." Many early floristic works include species abundance data that indicate advanced invasion success by this definition. However, distribution maps documenting species's spread for larger areas were not produced until the second part of the 20th century as Pyšek and Prach (2003) show for the Czech Republic. In contrast, the IUCN and other approaches in environmental policies classify species as invasive when these induce negative impacts on biodiversity and/or effect socioeconomic damage (Pyšek et al. 2020a). Such negative invasion impacts had been already addressed in the 19th century. Darwin (1859: 380), e.g., mentioned profound changes to the biota of oceanic islands such as a decrease in native species, driven by naturalized species, as "the first stage towards extinction". The German botanist von Chamisso (1827: 49) perceptively addressed invasion processes and related consequences about 30 years earlier:

> *"Where the civilized man settles, the view of nature changes ... His plantings and seeds spread around his dwelling ... In his gardens and fields, among the plants he cultivates, a multitude of other plants grow as weeds ... Where he has not taken all the space, the plants that were dependent on him move away from him, and even the wilderness, which his foot has not yet touched, changes its form."* [translation of all citations in German by IK]

Potential benefits of introduced species, beyond cultivated species, were considered only in the last decades in cost/benefit analyses (e.g., U.S. Congress 1993) and were later included in impact assessment schemes, highlighting the significant relationship between impact assessment and societal values (Bartz et al. 2010; Jeschke et al. 2014). Schlaepfer et al. (2012) emphasized the often underestimated conservation benefits of non-native species, and Dickie et al. (2014) illustrated the relevance of non-native species to socioeconomic sectors. Another recent topic of study is the context-dependence of invasion impacts. These impacts differ across biogeographic and ecological contexts. However, whether a change due to introduced species is regarded as a benefit or damage (or as a neutral effect) is also a question of whether it supports or conflicts with a particular set of values, which often differ within and between societies (Bartz et al. 2010). Context-specific assessments of plant invasions represent a challenge in invasion science (Pyšek et al. 2020b) and need to bridge ecological and societal realms (Sax et al. 2022).

Our ways of assessing invasion impacts in different contexts also likely have an older, yet largely hidden history. As a step towards illuminating these roots of invasion science, this paper analyzes an 18th-century example, included in a book by Christian Ludwig Krause (1706–1773) published 250 years ago (Krause 1773). Herein, Krause described the spread of the North American annual *Erigeron canadensis* L. (syn. *Conyza canadensis* (L.) Cronquist, Canadian horseweed) in a Central European landscape. He presented mechanisms of spread and associated ecological consequences, and he assessed the latter in terms of benefits and harm.

This is an intriguing case as *E. canadensis* is now the most widely spread non-native species in Europe (Lambdon et al. 2008) and beyond (e.g. Xu et al. 2012), colonizing a broad range of anthropic and (near)-natural ecosystems such as arable fields (Zimmermann et al. 2015), old fields (Prieur-Richard et al. 2000; Liendo et al. 2021), post-industrial sites (Zaplata et al. 2011; Anibaba et al. 2023), urban habitats (Dyderski and Jagodziński 2016), grasslands (Axmanová et al. 2021), coastal dunes (Giulio et al. 2020), floodplains (Anđelković et al. 2022), and other open sites, often with species-poor communities (Padullés Cubino et al. 2022). Due to its rapid spread, *E. canadensis* is often described as invasive and can create an economic burden in agricultural systems (Bajwa et al. 2016).

Here, the historical background of 18th-century Brandenburg, now part of Germany, is outlined first, including major environmental challenges of the time. Then Christian Ludwig Krause is briefly introduced together with his connection to introduced species. The subsequent analysis of the *Erigeron* case study addresses these questions: (1) What mechanisms and (2) what ecological consequences of spreading *E. canadensis*

did Krause describe, and to what extent does current knowledge support his insights? (3) How did he address invasion impacts in terms of benefits and harms and can this case be understood as an early precursor of context-dependent invasion assessments?

Historical background

18th-century Brandenburg

Eighteenth-century Brandenburg, today part of Germany, belonged to the Kingdom of Prussia, with Berlin as capital. Prussia's increasing political and economic importance fueled heavy demand for wood as the main building material and energy source. Many forests were converted to agricultural land to nourish the quickly growing population (Hasel and Schwartz 2006). In consequence, only about a quarter of Brandenburg's surface (24.3%) remained covered by forest by the end of the 18th century (Bratring 1804, p. 13). As elsewhere in Europe (McGrath et al. 2015), many of these forest remnants were degraded by manifold uses, resulting in their fragmentation and conversion into grasslands, heaths and fields (Krausch 1968). Over-grazing stimulated wind erosion on exposed sandy sites, rendering adjacent fields unusable due to flying sand. Around 1782, 23 open sand areas, including shifting dunes, each larger than 26 hectares, were documented around Berlin (von Klöden 1832). A major environmental challenge was thus to stabilize the open sand plains and restore agricultural land use and forests.

Christian Ludwig Krause

Christian Ludwig Krause (1706–1773) was renowned among his contemporaries as an influential gardener and owner of a commercial nursery and seed trade in Berlin, which was associated with a highly diverse garden (Kowarik 2023a). A plant directory by Roloff (1746) shows that Krause's garden harbored 2,420 taxa. The garden had been addressed as a privately-owned botanical garden and had more taxa than some other German botanical gardens at the time (Kowarik 2023a). Krause was considered one of the most important German gardeners in the 18th century (Teichert 1865), and his garden was particularly famous as a hub of cultivation and for distribution of newly introduced species (Nicolai 1779). Krause was the first in Berlin to cultivate several introduced species, including *Acer monspessulanum*, which has started to spread only recently (Kowarik 2023b), and others that spread earlier such as *A. saccharinum*, *Catalpa bignonioides*, *Gleditsia triacanthos*, *Myrica cerifera*, and *Pinus strobus*. Krause distributed plants and seeds across Germany and neighboring countries and participated in a supra-regional network of natural history research, centered around Carl von Linné with whom he corresponded for more than 20 years (Dietz 2010; Kowarik 2023a).

Krause published his main work, a 782-page book with horticulture as the focus (Krause 1773), 250 years ago. But the monumental work goes beyond horticulture, with some chapters addressing solutions for pressing environmental challenges of the

time (Kowarik in press): Krause described ways to restore oak woodlands, establish silvicultural pine plantations and hedgerows, and recover degraded land. In one chapter, he reported the natural revegetation of open sand fields by *Erigeron canadensis*, using the name "*Virga aurea*, *Virginiana annua*" (sensu de Tournefort 1698: 173)—an early report on biological invasions in a rural context.

Methodological approach

The chapter that reports on the *E. canadensis* case (Krause 1773: 405–409) is first evaluated here in terms of the included information on the occurrence of the species, mechanisms of spread, and associated ecological consequences, and how Krause related the latter to benefits or harms. The historical evidence is then contrasted with the current state of knowledge, based on a literature search in the Web of Science and on Wein's (1932) historical study of the introduction and spread of *E. canadensis* in the 17th and 18th centuries.

Results and discussion

Krause's report on *E. canadensis* invasion and related consequences

Krause wrote that the annual species was "brought to us about a hundred years ago". He was aware of the introduced status of *E. canadensis* and its North American origin since the species' name included a reference to North America, specifically Virginia, and the synonymous name mentioned Canada ("Aster *Canadensis annuus*, flore pappose", p. 407). He said that the quantity of seeds produced would "surpass all other species to [his] knowledge" (p. 407) and precisely described the morphological adaptation of "seeds" [achenes] for wind dispersal, which allows them to be "lifted by the air and carried away and borne by wind and storms over many miles" (p. 406). Krause reported highly abundant populations on degraded sandy areas in Brandenburg. He himself "encountered many thousands of plants in certain areas on sandy plains, where they have grown up to three feet [approximately 1 m] high and formed small shrubberies without having been sown" (p. 407).

Krause described benefits associated with *E. canadensis* invasions in sandy areas and illustrated underlying ecological mechanisms related to erosion control, soil formation and the facilitation of subsequent species (p. 407f.). While the species may not be suitable as a fodder plant, he said, "it has its true usefulness in sandy areas where it seeds itself." After it "has emerged in the spring, the wind has no power to pick up the sand and drive such towards good fields; instead, the growth of these plants creates firm and cohesive soil." "As soon as the plants have produced stems, leaves and other light nutritious bodies carried by the wind are deposited among them. These, together with the entire plant that dies in autumn, are dissolved by winter moisture, rain, and snow, and serve as nourishment for other plants, also brought by the wind, which then grow and find sustenance on the sand plains."

Finally, Krause contrasted the benefits of colonizing sand plains with the disservices of *E. canadensis* in gardens (p. 408): "Although this contemptible weed in gardens is of no use due to its astonishing proliferation, only causing much work with weeding and uprooting, it has its true value on light sandy fields."

Krause's insights in light of current knowledge

Introduction history and spread

Krause correctly identified the time of *E. canadensis*'s introduction ("about a hundred years ago", p. 407). Introduced from French colonial territories in North America, *E. canadensis* had probably initially been cultivated in French gardens (Wein 1932). However, the first record was in 1646 from the botanical garden in Altdorf near Nuremberg, Germany (Wein 1932). The species was also an early garden plant in Brandenburg (Gleditsch 1737), growing in Krause's garden in Berlin as well (Roloff 1746, p. 173). Wein (1932) explains why *E. canadensis* was cultivated as a garden plant from the mid-17th century into the 18th century, despite its unremarkable appearance. At that time, there was a fervor for all things French, so the species was positively regarded due to its origin from French colonies and its further distribution through France.

Krause's invasion report about *E. canadensis* is not the first. As early as 1659, its spontaneous spread was documented in the surroundings of Paris. It was described as "la plus commune de la campagne" [the most frequent of the countryside] by the end of the 17th century (de Tournefort 1698: 542). *Erigeron canadensis* was recognized as having escaped from cultivation in other European countries as early as the beginning of the 18th century, including in Brandenburg (since 1710; Wein 1932). Willdenow (1787: 270) described it in his Flora of Berlin as very common in gardens, cultivated fields, disturbed sites, and forests. While the spread of *E. canadensis* was thus previously known, Krause's report is probably the first one to mention abundant dominant populations in sandy areas and to describe associated ecological mechanisms and consequences.

Seed production and dispersal

The significance of copious seed production and long-distance dispersal by wind for the rapid spread of the species was recognized early by French botanists (de Tournefort 1698: 174). Recent studies support the high seed production of *E. canadensis*, which Krause described as surpassing all known species. A 1.5 m tall plant can produce nearly 230,000 seeds, and even a 40 cm tall plant can produce 2,000 seeds (Weaver 2001). In addition, European plants set more seeds, grow taller, and suffer less from co-migrated specialist enemies compared to American plants (Abhilasha and Joshi 2009).

The wind dispersal reported by Krause over "many miles" is also supported by current studies. Seed trap experiments revealed that while 99% of seeds fell within 100 m, some were moved at least 500 m (Dauer et al. 2007). For seeds lifted 10 m above

the ground, dispersal of up to 36.5 km was modeled under weak wind conditions (1–4 m s^{-1}), and up to 165 km under stronger wind (5–7 m s^{-1}), with 14% of seeds being moved more than 10 km (Liu et al. 2018). Considering that seeds have been detected at heights of 140 m, where they can reach the Planetary Boundary Layer and its wind speeds of over 20 m/s, dispersal of more than 500 km is feasible (Shields et al. 2006). This well explains the rapid spread after initial introduction in gardens and its wide distribution across Europe as already suggested by Wein (1932).

We now recognize that human-mediated seed dispersal plays a role in quickly establishing large dominant populations, for example through seed attachment to shoes or vehicles. Accordingly, Zaplata et al. (2011) explained the sudden occurrence of dense *E. canadensis* stands in post-mining sites by seed influx through trucks. In fact, seeds of this species were the second most commonly transported by traffic in Berlin, surpassed only by rye seeds from transport losses (von der Lippe and Kowarik 2007a, b). The dominant stands described by Krause could, therefore, have resulted from a combination of different dispersal pathways that were not fully understood in the 18th century.

Erosion control and soil improvement

Krause's report on the reduction of wind erosion on open sandy areas owing to dense *E. canadensis* stands appears plausible, and he is likely the only one describing this benefit for agricultural land use. Recent studies confirm the occurrence of *E. canadensis* in various environments with sandy soils across Europe (Zaplata et al. 2011; Zimmermann et al. 2015; Giulio et al. 2020; Axmanová et al. 2021). Although wind erosion in agricultural systems remains a significant and economically relevant problem today (Riksen and De Graaff 2001), erosion control by *E. canadensis* has not been considered in modern times. The wealth of existing literature on agricultural fields mostly focuses on negative consequences, such as yield losses due to competition with crops (Bajwa et al. 2016).

Current studies support the soil improvement highlighted by Krause through the capture of airborne material and the decomposition of its own biomass. Although *E. canadensis* has a lower decomposition rate than other pioneer plants, with a C/N ratio of 13.3 for leaf and 23.3 for litter (Schädler et al. 2003), it likely enhances soil formation and nutrient status on open sandy soils, particularly in the absence of other species. *Erigeron canadensis* invasions correlate with increased nutrient levels (N, P), decreased salinity, and improved soil structure in steppe soils (Zhang et al. 2021). Experiments have demonstrated soil nutrient content and enzymatic activities increasing with the abundance of *E. canadensis* (Zhang et al. 2020).

Facilitation of other species

Krause has described how abundant populations stimulate soil formation and nutrient enrichment on open sandy soils, thereby creating the foundation for the establishment of other species. This corresponds to the successional model of "relay floristics" described by Egler (1954) for old fields, where pioneer species prepare the site for

subsequent species, which then outcompete them. Facilitation of other species, as diagnosed by Krause, is indirectly confirmed by long-term successional studies. On both old fields (Schmidt 1981; Bonet and Pausas 2004; Dölle et al. 2008) and sandy pioneer sites in post-mining landscapes (Zaplata et al. 2013; Schaaf et al. 2013), the dominant *E. canadensis* and other annuals are largely replaced by perennial species after a few years. Therefore, Albert et al. (2014) recommend allowing succession in sandy old fields as a promising pathway to grassland restoration, despite the initial dominance of non-native annuals and given the proximity of target species.

Different abundances of *E. canadensis* might also induce different effects on plant community composition (Wang et al. 2021). A few conflicting experimental studies indicate negative, positive, or neutral effects, related to allelopathic effects (Shaukat et al. 2003; Djurdjević et al. 2011) and changes in soil biota (Řezáčová et al. 2020, 2021, 2022). However, it remains to be clarified whether changes in local communities caused by *E. canadensis* will lead to a long-term decline in species beyond the local level, potentially posing a threat to biodiversity. While the species frequently occurs in dry grassland on sandy soils in Brandenburg, negative effects on species of conservation concern are not expected since it usually temporarily colonizes gaps following disturbance (D. Lauterbach, personal communication, Fig. 1).

Figure 1. Decaying population of *Erigeron canadensis* in a dry grassland site in western Brandenburg (near Gülpe), previously subjected to mechanical disturbance (Photo by Daniel Lauterbach, October 2023).

Conclusions

Examining historical roots of current invasion science provides insights into the early perceptions of invasive species, allows us to trace the evolution of the discipline over time and helps contextualize modern research findings. Early historical roots of invasion science, since the 17th century, mainly focused on the introduction, spread, and naturalization of species. The negative impacts of biological invasions have been addressed only since the 19th century, but potential benefits have not received much attention–if any. Thus, Krause's 18th-century chapter on the colonization of degraded sand areas by *E. canadensis* is more than just an early account of plant invasions in the pre-industrial cultural landscape. It is one of the first known works on the benefits associated with plant invasions, covering a range of regulating ecosystem services such as erosion control, increase in soil fertility, and the revegetation of degraded land (Fig. 2).

Krause refrained from making assessments based solely on the copious abundance of *E. canadensis*, nor did he categorize the species as inherently undesirable or beneficial. Instead, he considered its different effects in various ecosystems, making his work an early example of a context-dependent assessment of plant invasions. He reported *E. canadensis* as a troublesome weed in gardens, which aligns with the current perspective on the species as an agricultural weed (Bajwa et al. 2016). At the same time, he demonstrated the beneficial effects of *E. canadensis* invasion in another land-use system, specifically in the recovery of degraded rural landscapes. Conducting such differentiated, nuanced assessments in different ecological and socioeconomic contexts is challenging in invasion research today (Bartz and Kowarik 2019; Pyšek et al. 2020b) as is the consideration of many unexploited opportunities to consider benefits introduced species can support (Sax et al. 2022).

Threats to biological diversity due to plant invasions were not yet a topic during Krause's time due to the prevailing utilitarian view of nature's benefits (Meyer and

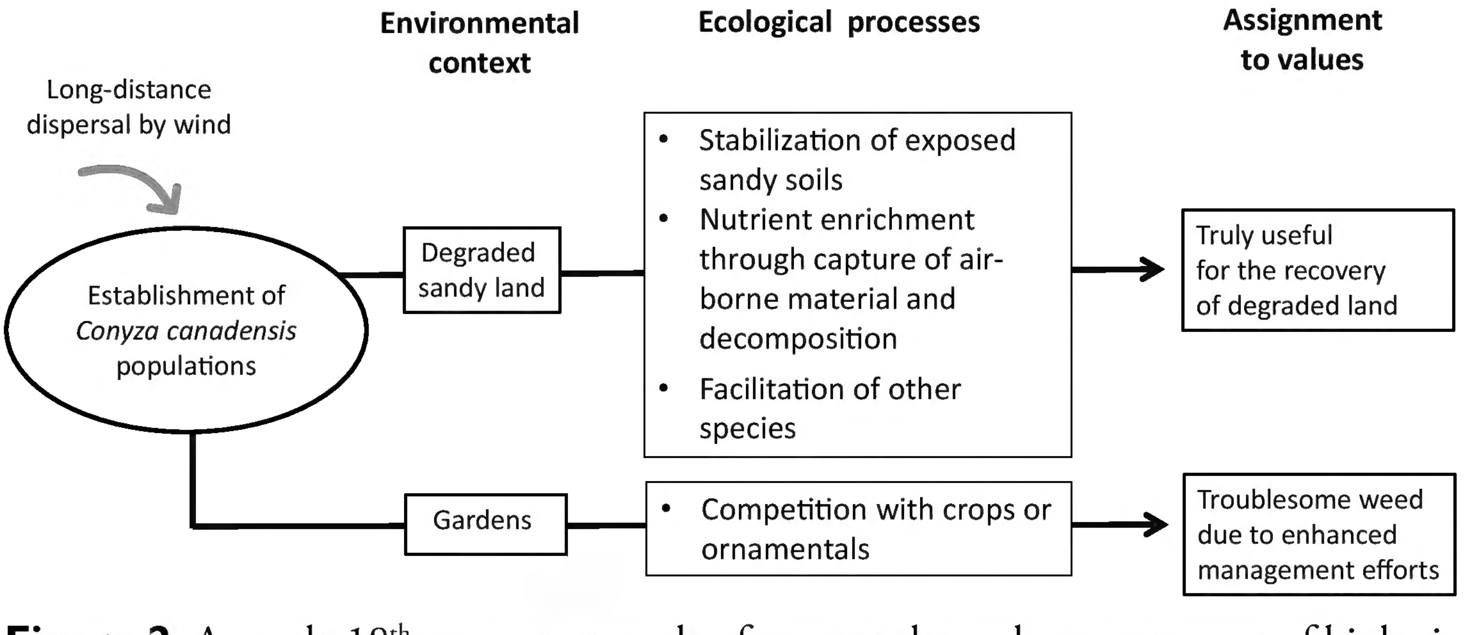

Figure 2. An early 18th-century example of context-dependent assessment of biological invasions: Invasions of different land-use systems by *Erigeron canadensis*, underlying ecological mechanisms, and their evaluation in the work by Krause (1773).

Popplow 2004). Current ecological studies indicate that, at least in the European context, the dominance of *E. canadensis* in sandy and other open habitats is largely caused by disturbance and does not hinder the recovery of species-rich, perennial vegetation. Allowing succession can thus even be a promising pathway for restoration (Albert et al. 2014).

It remains an open question whether the establishment of low-abundance populations of *E. canadensis* across many vegetation types in Europe with possible effects on neighbouring species actually challenges species conservation at the community or landscape levels. The example of Krause's work may encourage assessments of *E. canadensis* not solely based on its occurrence or frequency, but on demonstrated ecological effects and their associated benefits or harms. As Krause impressively demonstrated 250 years ago, these effects can differ starkly in different contexts, arguing for multiple responses to the same species.

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